SHARKS, RAYS AND A CHIMAEROID FROM THE KIMMERIDGIAN (LATE JURASSIC) OF RINGSTEAD, SOUTHERN ENGLAND

by CHARLIE J. UNDERWOOD

ABSTRACT. Sampling of a lenticular concentration of vertebrate debris and associated sediments from the lower Kimmeridgian of southern England has allowed the study of a diverse and abundant assemblage of chondrichthyan remains. A number of previously undescribed species are recorded, of which three new species are named; *Squatina*? *frequens*, *Synechodus plicatus* and *Protospinax planus.* Additional diagnosis of the genus *Paracestracion* Koken is given to allow its identification from dental remains. Several nominal batoid species are synonymised with *Spathobatis bugesiacus* Thiolliere. This assemblage is considered to be typical of Middle–Late Jurassic neritic environments, and is compared to other contemporaneous selachian faunas.

KEY WORDS: chimaeroid, Dorset, Jurassic, Kimmeridgian, ray, shark.

RECORDS of fossil sharks and rays from the Jurassic have largely been restricted to descriptions of material preserved as entire skeletons or isolated teeth and fin spines of large species. Few studies have concentrated on the isolated teeth of smaller taxa, with this work generally being incomplete in its coverage of faunas (e.g. Thies 1983; Candoni 1993; Thies and Candoni 1998). Despite this poor systematic coverage, it is evident that the Jurassic represented a major period of radiation of the Neoselachii, with many extant groups being present by the end of the period.

GEOLOGICAL SETTING

Upper Jurassic sediments are well exposed along the coast of Dorset, southern England. At Ringstead village, Oxfordian sandstones, limestones and mudstones of the Corallian Group are overlain by Kimmeridgian mudstones of the Kimmeridge Clay (Text-figs 1–2). A minor basal Kimmeridgian hiatus (Wignall 1990*a*) is succeeded by dominantly sandy and shelly clays, which pass upward into the laminated neritic mudstones typical of most of the unit. This basal interval is best included in the Kimmeridge Clay on lithological (first appearance of laminated black mudstones) and historical grounds; the recent inclusion of this interval in the Corallian Group (Newell 2000) is considered here as unnecessary and misleading.

Within the *cymodoce* Zone, two laterally continuous muddy sandstones, the Wyke and Black Head siltstones, are present. These sandstones are intensely bioturbated and both have an erosive base. This is especially evident within the Black Head Siltstone, where an underlying unit of black mudstone is seen to be cut out over the width of the exposure. Between these two coarser units, a lenticular horizon of shelly sandstone with numerous reworked phosphate granules records the presence of a third erosion surface. Where intervening sediment had been eroded, this bed was seen to become incorporated into the base of the Black Head Siltstone. The sedimentary architecture is therefore considerably more complicated than the single erosion surface noted by Newell (2000).

MATERIAL AND METHODS

The bulk of the vertebrate material studied was extracted from a lenticular calcareous sandstone between the Wyke and Black Head siltstones, in places being incorporated into the base of the latter. This lens is up

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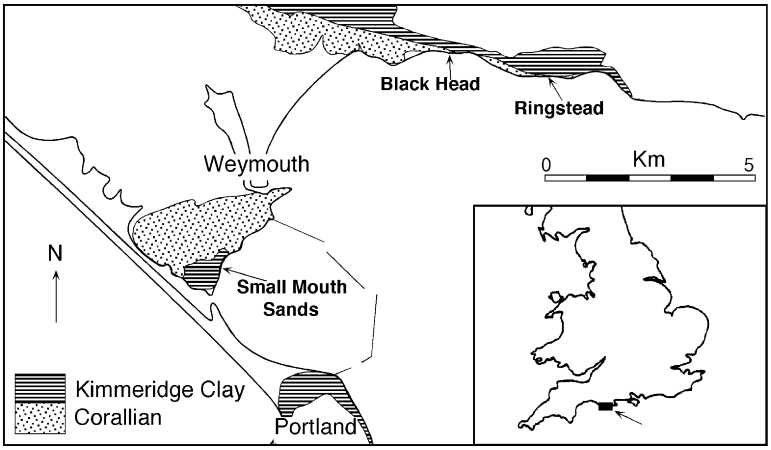
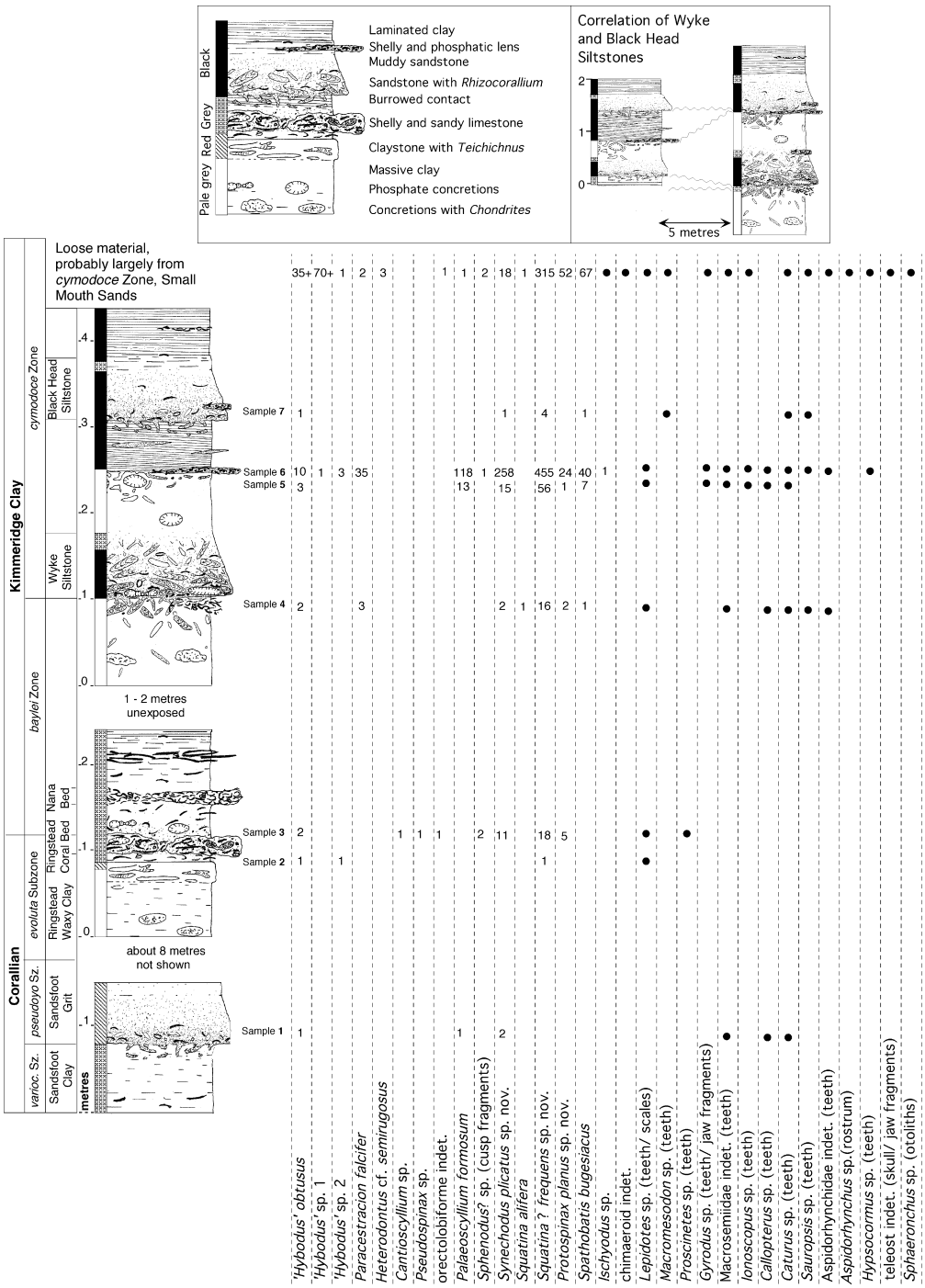


TEXT–FIG. 1. Map showing the locations of sites at Ringstead, Black Head and Small Mouth Sands.

to 5 cm thick, contains abundant oysters as well as a diverse fauna of other molluscs, and is extremely rich in small granules of reworked phosphate. Most of the material studied came from an exposure immediately to the east of the caravan site at Ringstead. This exposure has subsequently been obscured by sea-defences and steps. A second occurrence of the lens was recognised immediately to the east of the present end of the sea-defences in the autumn of 1998, but was subsequently removed by storm erosion. It is possible that future erosion will reveal more exposures of this lens. Further samples were collected from the immediately underlying mudstone, although it is likely that many of the teeth obtained from this unit came from burrow fills originating from above. A lens of shell material from immediately below the Wyke Siltstone was also sampled, as was the sandy mudstone from the base of the Kimmeridge Clay. Several other phosphate-bearing levels within sandstones of the Kimmeridge Clay and the upper part of the Corallian Group at nearby exposures at Black Head were sampled, but proved to contain very few selachian remains or to be cemented with pyrite or quartz. About 25 kg of the lenticular sandstone was sampled, along with between 12 and 40 kg of each of the mudstone levels. Only very small trial samples were processed of other sandstones.

Some comparative material was studied from the Kimmeridge Clay of Small Mouth Sands in Portland Harbour. This is a well-known vertebrate site, with abundant chondrichthyan material (Dineley and Metcalf 1999, p. 405). Most of the fossils are found loose on the beach or by sieving beach sand below a vegetated and slipped slope. For this reason, material is only very loosely constrained stratigraphically in comparison to that from Ringstead, although it is probable that fossils originate from the same general stratigraphic interval. In addition to the taxa recorded in this study, other hybodont sharks, chimaeroids and actinopterygians have previously been recorded from this site (Dineley and Metcalf 1999, p. 405; Brockenshire, pers. comm. 1999).

The preservation of selachian material from the main sampled lens and the underlying mudstone is similar, with two distinct modes of preservation of the teeth being evident. Many teeth have either no root, or have it preserved as a pale and highly porous remnant. In all teeth studied in detail this is seen to be a result of intense boring by endolithic organisms (see Underwood *et al.* 1999*a*) and not due to incomplete development of the teeth. In other specimens, the root is black and smooth, with the foramina often filled with dark material. It is possible that the latter teeth, with secondary phosphate precipitated over the root, have been reworked alongside the other reworked phosphate nodules and phosphatised shell material. At least some of this material may have been transported from a shallower setting, as suggested by the presence of fragments of colonial corals and phosphatised oolitic sediment. Despite this probable reworking and transport, there is no evidence for strong abrasion of any of the material. Many teeth have become highly fractured after burial, with calcite cement filling the cracks. Removal of this cement



TEXT-FIG. 2. Stratigraphical succession at Ringstead showing the occurrences of chondrichthyan and other fish remains; vertical scale in metres.

during acid preparation has resulted in the breakage of a large proportion of specimens. Teeth with secondary phosphate were rarely observed within other samples. Much of the vertebrate material from the basal Kimmeridge Clay has been highly abraded suggesting considerable reworking.

In all studied samples, selachian material was less abundant than teeth, vertebrae and other bones of actinopterygian fish. Isolated teeth suggest that diverse actinopterygian faunas are present, containing the same general groups as those noted by Mudroch and Thies (1996) from the Kimmeridgian of Germany. No reptile material was recorded from Ringstead despite the relative abundance of reptile fossils at Small Mouth Sands.

Calcareous sandstones were dissolved in buffered 20 per cent acetic acid, with frequent removal of acid-extracted fossils to limit the dissolution of calcite cements within fractures. Mudstones were oven dried before being hand-sieved at 125 μm, the resulting residue then being placed in 10 per cent acetic acid to remove the majority of the shell material. Samples were then sorted and picked from size fractions down to 355 μm. Selachian material never comprised a major part of the resulting residue because of the high relative abundance of grains of phosphate and quartz, pyrite and actinopterygian vertebrae.

Figured specimens were coated with gold-palladium alloy and observed with a scanning electron microscope (SEM). All figured specimens are deposited in the Department of Palaeontology at The Natural History Museum, London.

SYSTEMATIC PALAEONTOLOGY

The terminology used here for parts of the selachian teeth follows that of Cappetta (1987), with the nomenclature of the chimaeroid material following Patterson (1965) and Duffin and Reynders (1994). Synonymies given generally only include works that figure or mention teeth or other material that can be directly compared to specimens described here. Taxonomic relationships of the Neoselachii largely follow the work of Shirai (1996), with the placing of *Synechodus* within the Squalea following Duffin and Ward (1993), who suggested a close affinity with the Hexanchiformes.

Cohort EUSELACHII Hay, 1902
Superfamily HYBODONTOIDEA Owen, 1846
Family HYBODONTIDAE Owen, 1846

Genus 'HYBODUS' Agassiz, 1837

Type species. *Hybodus reticulatus* Agassiz 1837 from the Lower Jurassic of southern England.

Remarks. The genus *Hybodus* has been used to accommodate a large number of species, with only a small proportion having a similar dentition to *H. reticulatus*. It is, therefore, probable that few of these species should be included in *Hybodus*, but the genus is retained for the species figured here until a taxonomic revision is undertaken.

EXPLANATION OF PLATE 1

All specimens from lens between Wyke and Black Head siltstones unless stated otherwise.

Fig. 1. '*Hybodus*' sp. 1, P. 65670, labial view, preserved height 7·6 mm; ×7·5.

Fig. 2. '*Hybodus*' sp. 2, P. 65671, labial view, preserved width 10 mm; ×5·5.

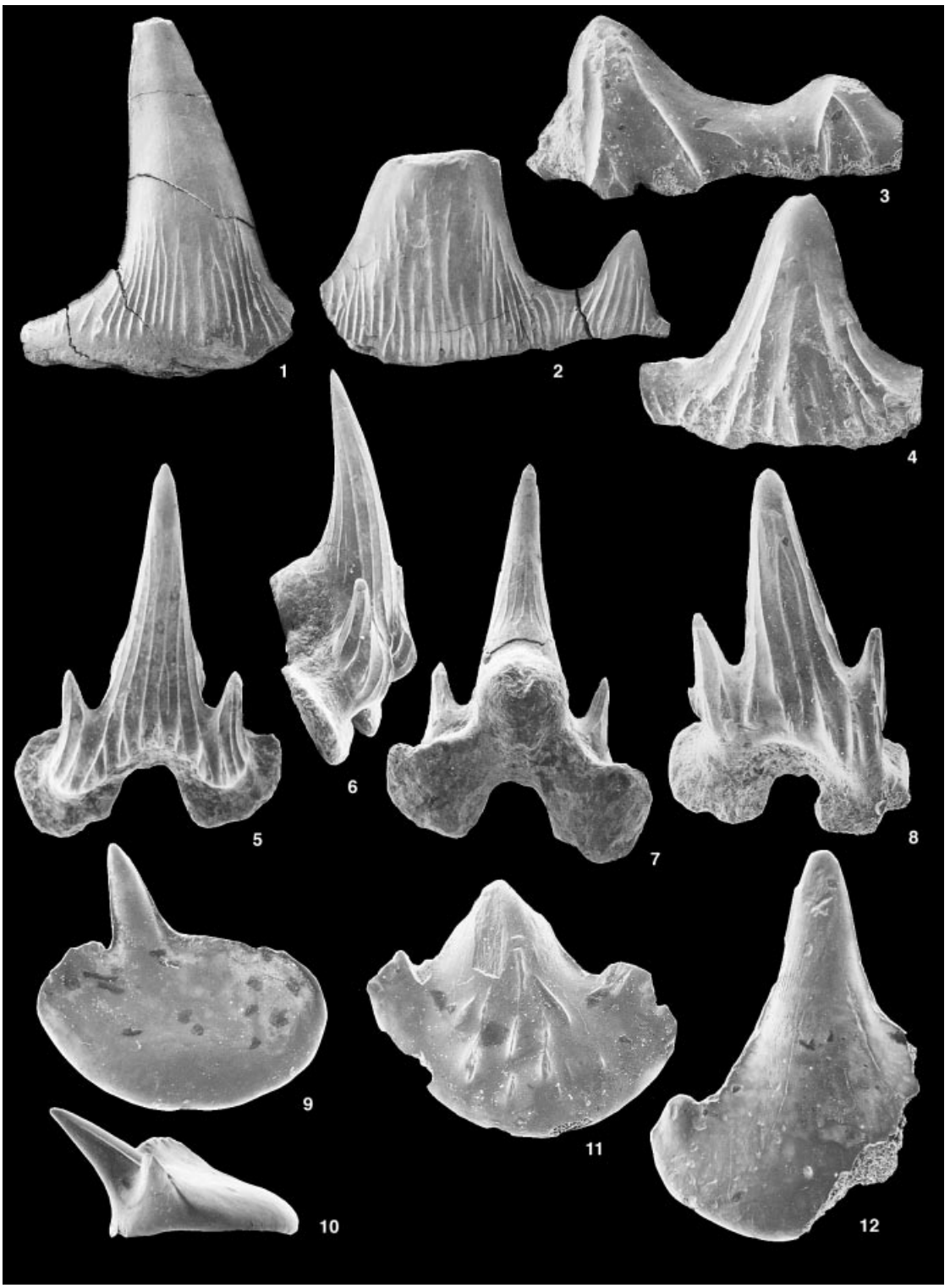
Figs 3–4. '*Hybodus*' *obtusus* Agassiz, 1843. 3, P. 65673, partial lateral tooth of juvenile, labial view, preserved width 1·7 mm; ×36. 4, P. 65672, partial anterior tooth of juvenile, labial view, preserved height 1·5 mm; ×26.

Figs 5–8. *Palaeoscyllium formosum* Wagner, 1857, P. 65675, anterior tooth, height 1·6 mm; ×32·5. 5, labial view. 6, lateral view. 7, lingual view. 8, P. 65676, lateral tooth, labial view, height 1·4 mm; ×41.

Figs 9–10. *Pseudospinax* sp., P. 65678, base of Kimmeridge Clay, width 1·1 mm; 9, labial view. 10, lateral view; ×41.

Fig. 11. *Cantioscyllium* sp., P. 65677, base of Kimmeridge Clay, labial view, width 0·9 mm; ×55.

Fig. 12. Orectolobiforme gen. et sp. indet., P. 65679, base of Kimmeridge Clay, labial view, height 1·5 mm; ×41.



UNDERWOOD, *Jurassic sharks*

'*Hybodus*' sp. 1

Plate 1, figure 1; Text-figure 3B–D

?1871 *Hybodus grossiconus* Agassiz; Phillips, p. 307, figs 19–20.

Material. One incomplete crown P. 65670; also P. 65680 from Small Mouth Sands.

Description. The single cusp is high and relatively slender and somewhat compressed. A well-developed cutting edge continues over the cusp (except for the broken apex) and along the single preserved lateral blade. The lateral blade is short and tapers sharply. Ornament is restricted to the lower part of both labial and lingual faces of the tooth. On the labial face this consists of fine, regularly spaced, longitudinal folds, which do not reach the base of the crown. Some of these folds bifurcate. Similar folds on the lingual face are finer. The root is unknown.

Remarks. This species is similar to *'H'. grossiconus* Agassiz, 1843, *'H'*. sp (of Schaeffer and Patterson 1984) and *'H'. ensis* Woodward, 1916, being separated from them by the regular and widely spaced ornament and the absence of lateral cusplets.

Occurrence. Lens between Wyke and Black Head siltstones. Teeth of this morphology are relatively common at Small Mouth Sands.

'*Hybodus*' sp. 2

Plate 1, figure 2

1995 *Hybodus* sp. Candoni p. 39.

Material. Four partial teeth including P. 65671.

Description. A robust main cusp is flanked by at least one pair of small lateral cusplets, all of which are strongly compressed. A cutting edge is very well developed, especially on lateral cusplets. The labial face of the main cusp is ornamented with fine longitudinal folds, which were not observed to extend to the apex. Individual folds are relatively discontinuous and bifurcation is rare. These folds are stronger and more continuous on lateral cusplets, where they may reach the apex. The lingual face of the main cusp has finer and more continuous folds, whilst ornament on both faces of the lateral cusplets is similar. The root is unknown.

Remarks. The overall profile of the tooth is very similar to that of '*H.*' *ensis* Woodward, 1916, although differs from it in the possession of strong ornament on the lateral cusplets. It is possible that '*Hybodus*' sp. 1 and '*Hybodus*' sp. 2 are synonymous, the difference in ornament being within the range observed within other hybodont species (Maisey 1983). It is considered here, however, that these morphologies are likely to represent different taxa, as no intermediate forms were observed and they have very different relative frequencies at the different sites studied.

Occurrence. Ringstead Coral Bed and lens between Wyke and Black Head siltstones.

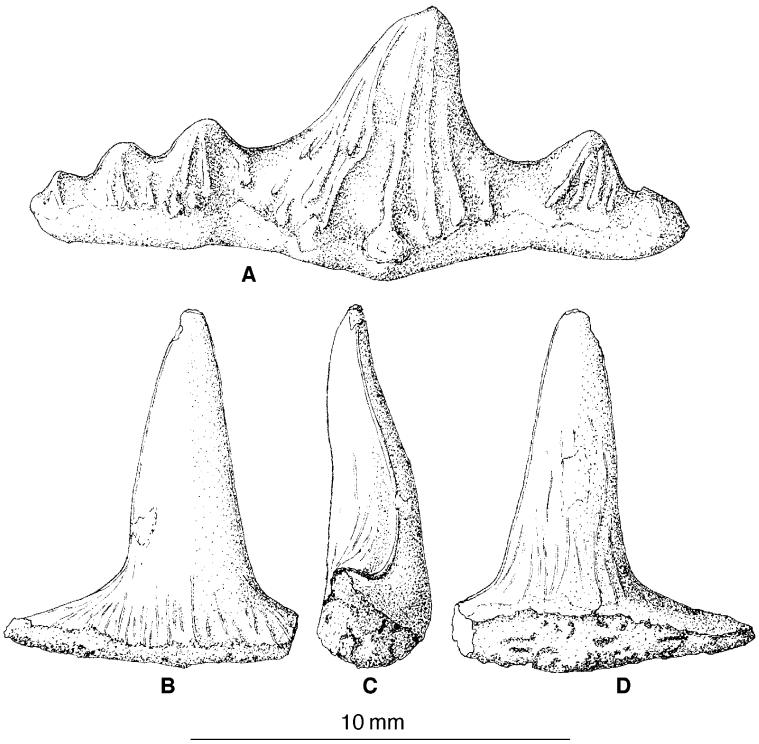
'*Hybodus*' *obtusus* Agassiz, 1843

Plate 1, figures 3–4; Text-figure 3A

1843 *Hybodus obtusus* Agassiz, p. 186, pl. 23, figs 43–44.
1889 *Hybodus obtusus* Agassiz; Woodward, p. 272, pl. 11, figs 8–13.
1991 *Hybodus obtusus* Agassiz; Martill, p. 197, pl. 36, fig. 8.
1995 *'Polyacrodus' obtusus* (Agassiz); Candoni, p. 39, figs 1–2.

Material. Fragments of at least 20 teeth including P. 65672; also P. 65674 from Small Mouth Sands.

Description. Fragments of teeth of a wide size range were recovered, but the overall similarity suggests that little heterodonty was present. The main cusp is rather low and triangular in profile, with 2–3 pairs of rather widely spaced



TEXT-FIG. 3. A, '*Hybodus*' *obtusus* Agassiz, 1843; P. 65674, Small Mouth Sands, lateral tooth, labial view. B–D, '*Hybodus*' sp. 1; P. 65680, Small Mouth Sands. B, labial view. C, lateral view. D, lingual view.

lateral cusplets decreasing in size laterally. The cusps are slightly compressed, with a very well-developed cutting edge, which continues unbroken over the occlusal edge. Strong and sharp-edged folds are present on the labial face of the cusps of most teeth. These bifurcate irregularly towards the base of smaller teeth, but only rarely divide in larger teeth. A well-developed fold covers a pronounced labial keel on the main cusp. These folds are widely spaced and reach the cusp apex in small teeth, becoming more numerous but less well developed in larger teeth. Similar but less well-developed folds are present on the lingual face. In the largest teeth (only seen as small fragments in this study), the folds may be partly lost and small swellings may be present at the base of the labial face of the tooth.

Remarks. '*Hybodus*' *obtusus* is well known from many Callovian–Kimmeridgian localities in northern Europe (e.g. Woodward 1889; Martill 1991).

Occurrence. Present in most samples. Teeth of '*H.*' *obtusus* are common at Small Mouth Sands.

Subcohort NEOSELACHII Compagno, 1977
Superorder GALEA Shirai, 1996
Order CARCHARHINIFORMES Compagno, 1977
Family SCYLIORHINIDAE Gill, 1862

Genus PALAEOSCYLLIUM Wagner, 1857, *non* Marck, 1863.

Type species. *Palaeoscyllium formosum* Wagner, 1857 from the Upper Jurassic of Germany.

Palaeoscyllium formosum Wagner, 1857

Plate 1, figures 5–8

1857 *Palaeoscyllium formosum* Wagner, p. 291.
1993 *Parasymbolus octevillensis* Candoni, pp. 148–155, text-figs 1–2, pls 1–3.
1994 *Parasymbolus octevillensis* Candoni; Candoni, pp. 48–52, figs 1–2, pl. 1–3.
1995 *Parasymbolus octevillensis* Candoni; Candoni, p. 38, figs 1–2.
1999 *Palaeoscyllium formosum* Wagner; Leidner and Thies, p. 34, figs 2B, 3F.

Material. 129 entire and partial teeth including P. 65675–65676.

Remarks. The specimens recorded here do not differ from material described in detail from the Kimmeridgian of northern France (Candoni 1993), and provide no additional taxonomic information. It has been shown (Leidner and Thies 1999) that the isolated teeth described by Candoni (1993) as *Parasymbolus octevillensis* are the same as those extracted from articulated skeletons of *Palaeoscyllium formosum* from German lithographic limestones. This indicated that the two species are conspecific and *Parasymbolus* is the junior synonym of *Palaeoscyllium.* *Parasymbolus reticularis* Underwood and Mitchell, 1999 from the Cretaceous of northern England should, therefore, also be referred to *Palaeoscyllium*.

Occurrence. Between Wyke and Black Head siltstones; also present but rare at Small Mouth Sands.

Order ORECTOLOBIFORMES Applegate, 1972
Incertae familiae

Genus CANTIOSCYLLIUM Woodward, 1889

Type species. *Cantioscyllium decipiens* Woodward, 1889 from the Upper Cretaceous of southern England.

Cantioscyllium sp.

Plate 1, figure 11

Material. One partial tooth P. 65677.

Description. The sole tooth appears to be from a posterior position in the jaw. The labial face of the crown is as wide as high, with a smooth semicircular basal edge. The occlusal edge has a triangular main cusp, about as wide as high. There are three poorly defined lateral cusplets, two to the anterior and one to the posterior. These are strongly flattened and appear to be outgrowths of the occlusal cutting edge. The labial surface is ornamented by a small number of short but strong folds. These appear to radiate from the base of the main cusp. The lingual face of the crown is unornamented, with a poorly defined uvula.

Remarks. *Cantioscyllium* is known from a number of species ranging from the Barremian (Kriwet 1999) to Campanian (Cappetta and Case 1999). This specimen allows the stratigraphical range of the genus to be extended into the Jurassic.

Occurrence. Base of Kimmeridge Clay.

Family HEMISCYLLIDAE Gill, 1862

Genus PSEUDOSPINAX Müller and Diedrich, 1991

Type species. *Pseudospinax pusillus* Müller and Diedrich, 1991 from the Upper Cretaceous of northern Germany.

Pseudospinax sp.

Plate 1, figures 9–10

Material. Single tooth lacking root P. 65678.

Description. The crown is thin and unornamented, and has an oval labial face, which is slightly expanded laterally. A single slender cusp projects lingually from the posterior part of the occlusal edge. A well-developed cutting surface is present either side of the cusp, being continuous over it. Posterior to the cusp this forms an incipient cusplet. The occlusal edge of the crown, and to a lesser extent the cusp, are angled labially to give a strongly concave crown surface. The lingual face of the crown is smooth and is slightly expanded to form a very weak uvula below the cusp.

Remarks. This species differs from *P. muftius* (Thies, 1983) in lacking lateral cusplets and having a labially projecting occlusal edge. This angled edge and the elongate cusp separate this species from *P. heterodon* Underwood and Mitchell, 1999, which it otherwise strongly resembles. The general form of the tooth crown is very similar to that of the extant torpedo ray *Benthobatis* (see Cappetta 1988, p. 43), but it is considered here that this similarity is superficial. Although the clade including the torpedo rays is predicted to have originated in the Jurassic (e.g. Shirai 1996), their known fossil record only extends through the Caenozoic, with the earliest known forms having teeth very different from those of *Benthobatis.*

Occurrence. Base of Kimmeridge Clay.

Gen. et sp. indet.

Plate 1, figure 12

Material. One partial tooth P. 65679.

Description. The preserved labial face of the crown is relatively triangular and slightly convex with a smoothly curved basal edge. Much of the height is made up of the main cusp, with at least one small lateral cusplet. A cutting edge is developed across both preserved cusps.

Remarks. This poorly preserved tooth is of typical hemiscylliid morphology and somewhat resembles the extant genus *Chiloscyllium*. Similar teeth have been recorded in the Toarcian (Delsate and Lepage 1990, fig. 1.4) and Aalenian (Thies 1989, figs 3, 5).

Occurrence. Base of Kimmeridge Clay.

Order HETERODONTIFORMES Berg, 1940
Family HETERODONTIDAE Gray, 1851

Genus PARACESTRACION Koken (*in* Zittel), 1911

Type species. *Cestracion falcifer* Wagner, 1857.

Diagnosis based on dental material. Very strongly heterodont. Teeth of juveniles and anterior teeth of mature individuals have a flat labial surface with smoothly curved basal edge. The triangular central cusp is flanked by smaller paired lateral cusplets. The uvula is narrow and tapering but well developed. The root is low and holoaulacorhize, with basal faces narrow and curved. Some lateral and antero-lateral teeth of juvenile and immature individuals are similar but wider with cusps directed commissurally. Lateral teeth of mature individuals are 'molariform', with a wide and highly ornamented occlusal surface having a well-developed longitudinal crest.

Remarks. The genus *Paracestracion* was originally erected for *Paracestracion falcifer*, a species known from a number of complete and partial skeletons from the German Upper Jurassic. This was recognised as differing from extant species of *Heterodontus* in several respects (Koken 1911). Characters used for this initial definition of *Paracestracion* were subsequently recognised as being unreliable for generic diagnosis (Schweizer 1964; Maisey 1982). Despite this, *P. falcifer* differs from both extant *Heterodontus* species and the contemporaneous *H. zitteli* Eastman, 1914 in possession of partly vascularised fin spines and a more posteriorly positioned first dorsal fin (Maisey 1982). The lack of descriptions of the differences in dentition between *Paracestracion* and *Heterodontus* may have been one of the main reasons for the failure of some more recent workers to recognise *Paracestracion* as a separate genus (e.g. Thies 1983; Cappetta 1987).

The dentition of *Paracestracion* is very similar to that of *Heterodontus*, with pectinate anterior teeth similar to those of juvenile *Heterodontus*. This tooth morphology, however, is retained into adulthood in *Paracestracion*, and is not replaced by teeth with an elongate crown and a high hemiaulacorhize root typical of more mature *Heterodontus*. Molariform lateral teeth of *Paracestracion* are very similar to those of some species of *Heterodontus* (Maisey 1982), but their presence only in larger individuals (Schweizer 1964) and relative rarity in isolated assemblages suggests that they may develop at a later stage of ontogeny. The absence of molariform teeth from some assemblages (e.g. Batchelor and Ward 1989) may suggest that these teeth were never developed within some species of *Paracestracion*. As anterior teeth of juvenile *Heterodontus* are not readily distinguishable from teeth of *Paracestracion*, it is only in cases where teeth from non-juvenile individuals are present that generic identification can be carried out with certainty (this may be evidenced by the presence of a range of tooth sizes and/or the presence of molariform lateral teeth). The presence of anterior teeth characteristic of adult *Heterodontus* allow the genus to be recognised. If only pectinate anterior teeth are present within a population of different sized teeth, *Paracestracion* may be identified.

Recognition of a combination of dental characteristics unique to *Paracestracion* allows several additional species to be referred to this genus, giving it a stratigraphic range from Toarcian to Tithonian. These are: (1) *Heterodontus sarstedensis* Thies, 1983 from the Toarcian of Belgium (Delsate and Lepage 1990) and the Aalenian of Germany (Thies 1983); (2) an unnamed species from the Bathonian of England (Young 1982, fig. 2G–H, J–K, M–N); (3) *Heterodontus* sp. from the Callovian of England (Thies 1983; Martill 1991).

Paracestracion fin spines are known from the Callovian and Kimmeridgian of England (Maisey 1982). *Heterodontis zitteli* and *H. semirugosus* (Plieninger, 1847) are retained in *Heterodontus* due to skeletal and dental characteristics respectively, as are all described post-Jurassic heterodontiformes. '*Heterodontus*' *duffini* Thies, 1983 teeth bear little resemblance to those of any known heterodontiform and is almost certainly an orectolobiform.

Paracestracion falcifer (Wagner, 1857)

Plate 2, figures 1–9

1857 *Cestracion falcifer* Wagner, p. 290.
1964 *Heterodontus falcifer* (Wagner); Schweizer, p. 69, fig. 3, p. 112, figs 2–4.
1995 *Protospinax* sp.1; Candoni, p. 38, figs 1–2.

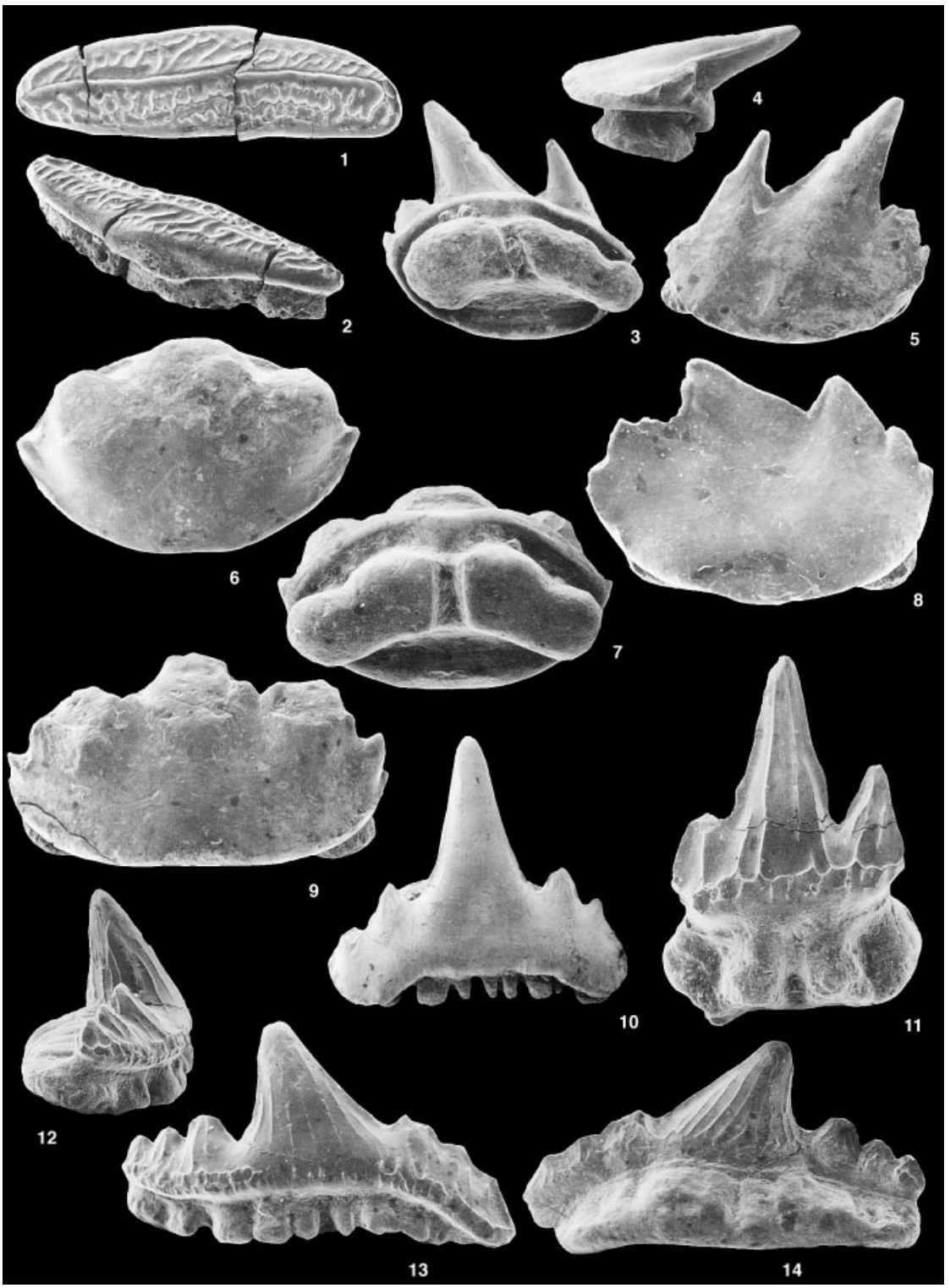
EXPLANATION OF PLATE 2

All specimens from lens between Wyke and Black Head siltstones.

Figs 1–9. *Paracestracion falcifer* (Wagner, 1857). 1–2, P. 65681, lateral tooth of adult, width 3·5 mm; ×17. 1, occlusal view. 2, oblique lingual view. 3–5, P. 65682, anterolateral tooth of juvenile, width 1·6 mm; ×26. 3, basal view. 4, posterior view. 5, labial view. 6–7, P. 65683, anterior tooth of adult, width 2·1 mm; ×26. 6, labial view. 7, basal view. 8, P. 65684, lateral tooth of juvenile, labial view, width 1·2 mm; ×45. 9, P. 65685, anterior tooth of adult, labial view, width 2·4 mm; ×25.

Figs 10–14. *Synechodus plicatus* sp. nov. 10, P. 65691, anterior tooth, labial view, height 3·7 mm; ×12. 11, P. 65687, symphyseal tooth, labial view, height 1 mm; ×36. 12–14, P. 65686, holotype, lateral tooth, width 3·2 mm; ×19. 12, posterior view. 13, labial view. 14, lingual view.

PLATE 2



UNDERWOOD, *Paracestracion*, *Synechodus*

Material. 36 anterior and juvenile teeth including P. 65682–65685; two lateral adult teeth including P. 65681.

Description. This species shows extreme ontogenetic and monognathic heterodonty. Adult lateral teeth are elongate in occlusal view, with the lingual edge being rather convex but the labial face being flat or slightly concave. The occlusal surface is traversed by a strong longitudinal ridge, which is displaced lingually. Somewhat irregular and sinuous ridges branch off this on the lingual side, with a finer and more reticulate ornament to the labial side. The crown is uniformly low with no ornament on the edges, and with the basal edge expanded into a weak uvula on the lingual side. The root is low and narrower than the crown, with the basal face being slightly curved with the convex side toward the lingual edge. At least two well-developed foramina are present on the lingual face of the root, but it is unclear whether the root is holoaulacorhize or hemiaulacorhize due to damage.

Anterior teeth have an oval, bilaterally symmetrical crown with well-developed cusps projecting lingually. In most teeth these cusps show intense wear, and have been almost completely removed in many specimens. Where present, the main cusp is triangular and at least as long as wide, usually being flanked by two pairs of lateral cusplets. The inner pair of cusplets is well developed whilst the outer pair, where present, are very small and project somewhat laterally. All cusps are rather flattened with well-developed cutting edges. The labial edge of the crown is smoothly curved. The lingual edge of the crown is narrow with a small central uvula, which is strongly triangular. The edge of the crown is somewhat flared in some teeth. The root is low, with the basal face being roughly parallel or at a low angle to the labial surface of the crown. It is shorter than the crown but of similar width, the basal face being relatively parallel sided and smoothly curved. This is cut by a strong nutritive groove in all teeth which has a large central foramen. Other foramina are small and largely confined to the lingual face.

Lateral and anterolateral teeth of juvenile and immature individuals are generally similar to anterior teeth. They differ largely in that the cusps are strongly angled to the posterior making the teeth far less symmetrical. The single well-preserved lateral tooth of a juvenile has short cusps and a rather concave labial face to the crown. Strongly elongated cuspate teeth, such as those noted by Schweizer (1967), were not found.

Remarks. The assemblage of teeth demonstrates a very similar range of morphologies to those noted by Schweizer (1964) in specimens from the Nusplinger plattenkalk. It is very likely that *Paracestracion* fin spines from the Kimmeridge Clay of the Weymouth area (Maisey 1982) are conspecific with this species. The high degree of wear on many of the teeth is typical of anterior teeth of *P. falcifer* immediately prior to their being shed (Schweizer 1964).

Occurrence. Immediately below Wyke Siltstone and lens between Wyke and Black Head siltstones.

Genus HETERODONTUS de Blainville, 1816

Type species. *Squalus philippsi* Schneider, extant.

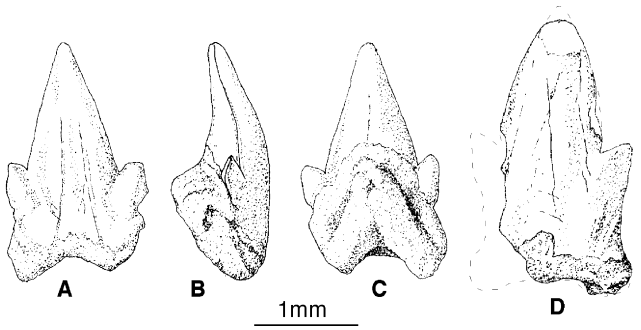
Heterodontus cf. *semirugosus* (Plieninger, 1847)

Text-figure 4A–D

1847 *Acrodus semirugosus* Plieninger, p. 227, fig. 17.
1852 *Hemipristis bidens* Quenstedt, p. 269, figs 21–22.
1961 *Heterodontus semirugosus* (Plieninger); Schweizer, p. 110, figs 1–3, 7–8; p. 111, figs 1–3.
1995 *Heterodontus* sp.; Candoni, p. 38, figs 1–3.

Material. Two imperfect anterior teeth: P. 65711 and 65712.

Description. The crown of the tooth has a rather triangular labial face, with about half of the height being made of the main cusp. A pair of smaller triangular lateral cusps project slightly laterally. The basal edge of the labial surface is strongly flared, giving a somewhat constricted shape to the labial part of the crown. A relatively strong lingual uvula is present. The root is relatively low and overhung by the crown on all sides. There is a strongly V-shaped basal face enclosing a large basal foramen. A pair of relatively well-developed lateral foramina is also present.



TEXT-FIG. 4. A–D, *Heterodontus* cf. *semirugosus* (Plieninger, 1847). A–C, P. 65712, Small Mouth Sands, anterior tooth. A, labial view. B, lateral view. C, lingual view. D, P. 65711, Small Mouth Sands, partial anterior tooth.

Remarks. These teeth compare very well to anterior teeth of *H. semirugosus* figured by Schweizer (1961). This species is included here for purposes of comparison with *P. falcifer* and to demonstrate the presence of a second heterodontiform in the Kimmeridge Clay of Dorset. It is possible that *H. zitteli* represents a juvenile specimen of this species, being only known from a single, very juvenile individual (Maisey 1982). It is likely that a *Heterodontus* fin spine from the Kimmeridge Clay of the Weymouth area (Maisey 1982) is conspecific with this species.

Occurrence. Rare at Small Mouth Sands.

Superorder SQUALEA Shirai, 1996
Order SYNECHODONTIFORMES Duffin and Ward, 1993
Family PALAEOSPINACIDAE Regan, 1906

Genus SYNECHODUS Woodward, 1888

Type species. *Hybodus dubrisiensis* Mackie, 1863 from the Upper Cretaceous of southern England.

Synechodus plicatus sp. nov.

Plate 2, figures 10–14; Plate 3, figures 1–5

1995 *Palaeospinax* sp.; Candoni, p. 39, figs 1–2.
1995 *Synechodus* sp.; Candoni, p. 39.

Derivation of name. From the folds on the crown of lateral teeth.

Holotype. P. 65686.

Material. 289 complete and partial teeth from all parts of jaw including P. 65687–65693.

Diagnosis. The dentition is highly heterodont. The crown of anterior teeth is symmetrical and as high as wide, with the robust main cusp with one or two pairs of very short but robust lateral cusplets. The labial face is largely unornamented other than some very fine longitudinal folds. The lingual face is unornamented. Anterolateral teeth have a crown wider than high. The central main cusp is angled to the posterior. One to three cusplets are present to the posterior of the main cusp. Three to four anterior cusplets are partially fused to give an irregularly serrated blade. Labial ornament consists of fine longitudinal folds, straight on the main cusp but more irregular and sinuous on lateral cusplets. Basally,

these folds divide to form a narrow band of reticulation. Lingual ornament is similar but finer. The thin and wide crown of posterior teeth has an occlusal ridge and may have the main cusp present as a central striated cone. Labially and lingually to this is a narrow band of reticulate ornament. The crown very strongly overhangs the root in all but the most posterior teeth. These are high and thick with a flat basal face in anterior teeth, becoming narrow and high posteriorly. Very strong, irregularly spaced, vertical folds are present on the labial face of the root.

Description. This species shows very strong gradient monognathic heterodonty, with the large number of specimens collected allowing a good approximation of the dentition to be reconstructed. Symphyseal teeth are small with a main cusp flanked by a pair of well-developed lateral cusplets. Cusps are all ornamented by few strong longitudinal folds, which branch off a single sinuous transverse fold near the base of the crown. The root is high and rather flared laterally, with a large foramen between a pair of globular projections of the labial face. Relatively bilaterally symmetrical teeth, other than from symphyseal files, are rare, which may suggest that they constituted only one or two anterior files. These teeth are large and, in contrast to all other teeth, very poorly ornamented. The labial face of the crown has a concave basal edge and rounded lateral edges. The main cusp is conical and robust, somewhat swollen at the base in some teeth. A weak but continuous cutting edge is present. Lateral cusplets are small, with either two pairs or one pair plus a pair of incipient cusplets. Ornament is poorly developed, consisting of 2–4 extremely faint longitudinal folds on the sides of the main cusp. The crown overhangs the root very strongly along its basal and lateral edges. The root is massive and has a flat basal face. It is strongly pseudopolyaulacorhize, with irregular longitudinal folds on the labial face. The lingual face is sloping and has very weak crenulations and numerous, irregularly spaced foramina. Anterolateral teeth are less symmetrical than teeth from the most anterior files. The crown is wider than high, with a central main cusp. This is conical and angled slightly to the posterior and may be slightly curved lingually. One to three lateral cusplets are present on the posterior side of the main cusp. These are short and conical, decreasing in size laterally. On the anterior side of the main cusp, up to four cusplets are present. These are strongly fused to give an irregularly serrated occlusal surface with a well-developed cutting edge. The crown is ornamented by fine longitudinal folds, which reach the apex of the cusps. Up to eight such folds are present on the labial face of the main cusp, slightly more on the lingual face. Similar but rather more irregular folds are present over both faces of the lateral cusplets, being finer on the lingual face. Towards the base of the crown, irregular bifurcation of the folds creates a narrow band of reticulate ornament. This reticulation is well-developed on the labial face below the lateral cusplets. It may also be present, but less well developed, on the lingual face and at the base of the main cusp of some teeth. The root is similar in the more anterior teeth, but wider and shallower with the crown being angled nearly at right angles to the basal face of the root. The crown of posterior teeth is wide and shallow. In some posterior teeth, a small central cusp is present, with both faces ornamented by irregular folds forming a reticulate pattern on the lower part of the face. Where no cusp is present, the occlusal face is flat other than a well-developed transverse ridge. This is flanked by paired strips of reticulation. The crown overhangs the root on all sides. The root is high and shallow, especially in commissural teeth.

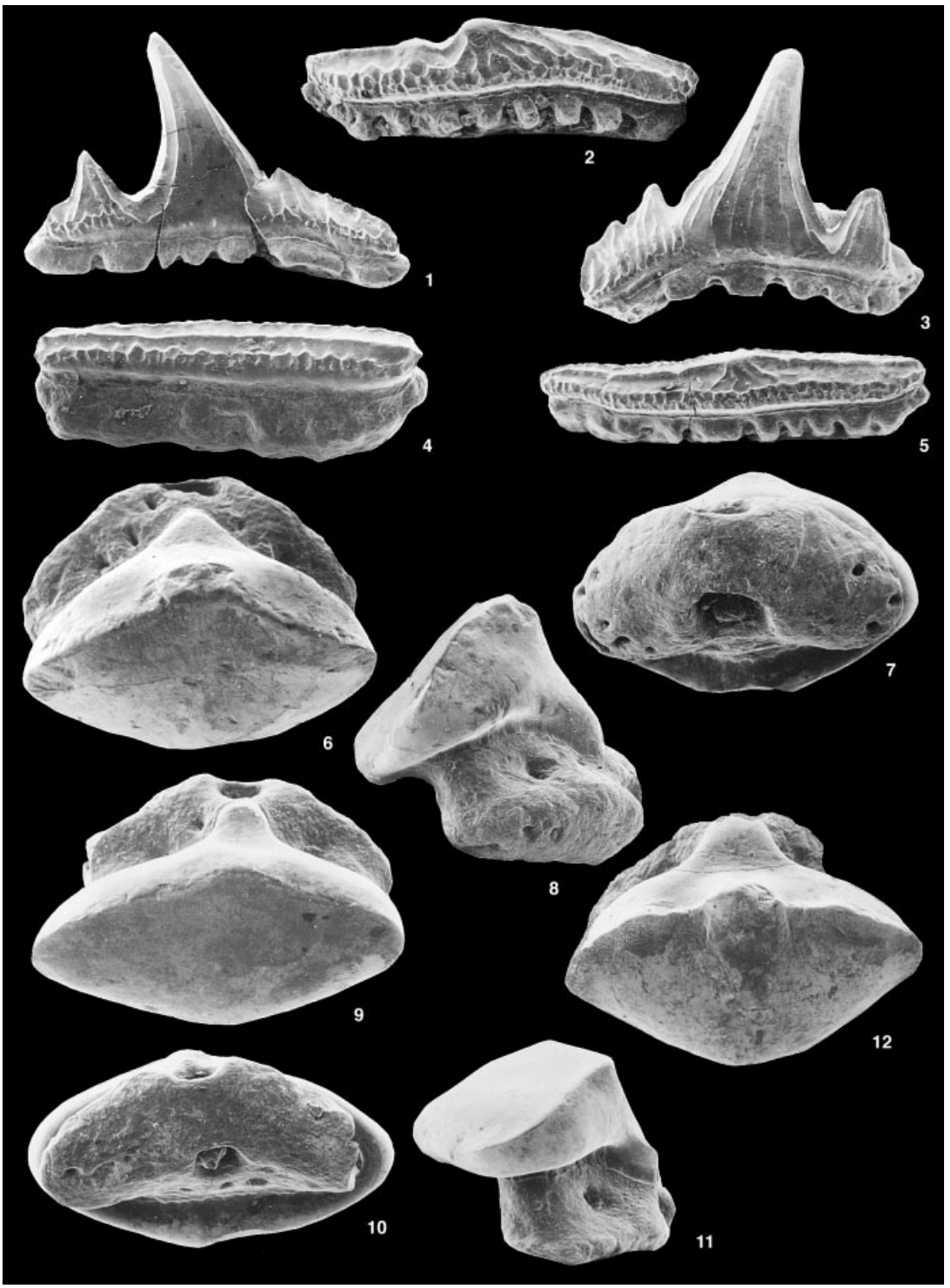
Remarks. Anterior teeth of *Synechodus plicatus* sp. nov. are similar to those of *S. riegrafi* (Thies, 1983), of which only anterior teeth have been figured, but differ in that teeth of *S. riegrafi* have higher lateral cusplets and an ornament of strong longitudinal folds which do not become reticulate at the base. Teeth of other species of *Synechodus* lack either the irregularly fused cusplets on anterolateral teeth or the reticulate ornament at the base of the crown. A lateral tooth figured as *Synechodus* sp. from the Upper Jurassic of Germany (Leidner and Thies 1999) and an anterior tooth described as *Paraorthacodus* sp. from the Upper Jurassic of France (Candoni 1995) are similar to *S. plicatus*, but differ in being considerably more symmetrical and lacking fusion of the anterior cusplets.

EXPLANATION OF PLATE 3

All specimens from lens between Wyke and Black Head.

Figs 1–5. *Synechodus plicatus* sp. nov. 1, P. 65693, anterolateral tooth, labial view, width 3·4 mm; ×14. 2, P. 65690, lateral tooth, labial view, width 3·3 mm; ×19. 3, P. 65692, anterolateral tooth, labial view, width 3·2 mm; ×17. 4, P. 65688, commisural tooth, oblique lingual view, width 1·5 mm; ×41. 5, P. 65689, posterior tooth, oblique labial view, width 3·3 mm; ×18.

Figs 6–12. *Protospinax planus* sp. nov. 6–8, P. 65694, holotype, anterior tooth, width 1·5 mm; ×36. 6, occlusal view. 7, basal view. 8, lateral view. 9–11, P. 65695, lateral tooth, width 1·7 mm; ×35. 9, occlusal view. 10, basal view. 11, lateral view. 12, P. 65696, anterior tooth, occlusal view, width 1·9 mm; ×30.



UNDERWOOD, *Protospinax*, *Synechodus*

Occurrence. Present in almost all samples studied; frequent at Small Mouth Sands.

Superorder HYPNOSQUALEA Carvalho and Maisey, 1996
Family PROTOSPINACIDAE Woodward, 1919
Genus PROTOSPINAX Woodward, 1919

Type species. Protospinax annectans Woodward, 1919 from the Upper Jurassic of southern Germany.

Protospinax planus sp. nov.

Plate 3, figures 6–12

?1990 *Protospinax annectans* Woodward, 1919; Batchelor and Ward, p. 193, pl. 3, fig. 3.
1995 *Squalogaleus* sp.; Candoni, p. 38.
?1995 ?Rajiforme *incertae familiae*; Candoni, p. 38.

Derivation of name. From the flat (as opposed to concave) labial face of the crown.

Holotype. P. 65694.

Material. 32 complete and partial teeth including P. 65695–65696.

Diagnosis. Dentition relatively heterodont, with all teeth being bilaterally symmetrical. The thin crown is oval in labial view, being wider than high, with a flat or very faintly convex labial face. There is a sharply angled contact between the labial and lingual face with a poorly developed cusp, which may be flanked by a pair of incipient lateral cusplets. A narrow but well-defined lingual uvula extends about half way down the lingual face of the root. The hemiaulacorhize root is high in anterior teeth, less so in lateral files, and somewhat displaced lingually. The root is almost as wide as the crown, with the basal face of the root being convex and slightly curved lingually. Centro-lingual and centro-labial foramina are very well developed, as is a single pair of lingual foramina.

Description. Anterior teeth are as high as wide, with the crown being rather erect, the angle between the labial face of the crown and the basal face of the root being up to 90 degrees. The labial face of the crown is rather wider than high, being almost flat with only a slight convexity near the cusp. The cusp is poorly developed, being little more than a triangular lingual termination of the crown. The labial face of this may be flat or slightly convex, and a single pair of incipient lateral cusplets is present in some teeth. The lingual face of the crown is rather low and is angled at about 90 degrees from the labial face, the contact being sharp but without a well-developed cutting edge. The base of the crown is flat other than where it extends basally to form a narrow but strong uvula, and strongly overhangs the root. The root is wide and relatively narrow, being displaced lingually. The lingual face of the root is concave with a swollen base. There is a very prominent foramen on the lingual face of the root immediately below the uvula, which connects to an equally well-developed foramen on the basal or labial face. Either side of the uvula is a large lateral foramen, which may rarely be replaced by two or three smaller foramina. Small foramina are also present on the lateral ends of the basal face and on the labial face of the root.

Lateral teeth are generally similar but are far lower in overall profile, with the labial face of the crown forming only a small angle with the basal face of the shallower root. The crown is considerably wider that high, with the cusp being little more than an angled lingual edge of the crown. The uvula is well developed but shorter than on anterior teeth, often with a wear facet at its contact with the crown. The root is lower than in anterior teeth, with a flatter and less swollen basal face. Foramina appear to be equally well developed in all teeth.

Remarks. The type species of *Protospinax*, *P. annectans* Woodward, 1919, is known from several complete skeletons from the Solnhofen Limestone of Bavaria (Carvalho and Maisey 1996). Teeth have been figured from two specimens, the adult holotype and a juvenile specimen (regarded as the type specimen of the genus *Squalogaleus* by Maisey 1976 and Cappetta 1987). The teeth of the juvenile specimen have been figured a number of times (Woodward 1919, fig. 3; Maisey 1976, text-fig. 8; Thies

1983, text-fig. 5; Cappetta 1987, fig. 55B–G), with both lateral and anterior teeth being represented. These are similar to teeth of *Protospinax planus* sp. nov., differing largely in being far smaller and having more strongly separated root lobes, with a nutritive groove being present in at least one tooth (Cappetta 1987, fig. 55F–G). Teeth of the adult specimen (Maisey 1976, text-fig. 2; Cappetta 1987, fig. 62B–F) differ from teeth of *P. planus* in possessing a very strongly concave labial face of the crown, rather better developed cusps which project labially, less well-developed uvula and a nutritive groove separating the root lobes. It is, therefore, evident that *P. planus* differs from *P. annectans* in retaining a flat labial face of the crown throughout ontogeny, and possesses a more robust root which was not observed to possess a nutritive groove. It is possible that very small and juvenile teeth, which were not recovered during this study, may, as in *P. annectans*, possess a nutritive groove. Teeth from the British Callovian referred to *P. annectans* by Thies (1983) appear to be closer to *P. planus* than *P. annectans*, but differ from it in having a far better developed cusp, lower root and mildly concave labial face of the crown in lateral teeth. Teeth from the British Bajocian and Bathonian (Young 1982, fig. 2E–F, I, L and pers. obs.) are also similar to those of *P. planus* sp. nov., but are at present too poorly known for comparison. *Protospinax lochensteinensis* Thies 1983 from the German Oxfordian and *P.* sp. from the German Toarcian (Thies, 1989) more closely resemble *P. annectans* than *P. planus*.

Occurrence. All Kimmeridgian samples below the Black Head Siltstone; frequent at Small Mouth Sands.

Family SQUATINIDAE Bonaparte, 1838

Genus SQUATINA Duméril, 1806

Type species. *Squatina squatina* Linnaeus, 1758.

Remarks. The genus *Squatina* is represented by a number of extant species which have very similar dentitions, and it has been suggested (e.g. Herman 1977) that species cannot readily be differentiated by tooth morphology. Teeth of Cretaceous–Recent *Squatina* are indeed very similar, but species can be distinguished. Well-preserved specimens of *Squatina* are known from the Upper Jurassic of Germany. The overall body morphology of these agrees well with extant taxa, but the teeth differ somewhat in detail from those of modern species (Leidner and Thies 1999). The tooth morphology of early species of *Squatina* is very similar to that of some genera of orectolobiforms, and it is therefore often difficult to assign species between these distantly related groups.

Squatina alifera (Münster, 1842)

Plate 4, figures 1–2

1842 *Thaumas alifer* Münster, p. 62, fig. 1.
1843 *Thaumas fimbriatus* Münster, p. 53, fig. 4.
1856 *Thaumas speciosa* Meyer, p. 418.
1859 *Squatina* (*Thaumas*) *speciosa* Meyer; Meyer, p. 4, fig. 2.
1991 *Palaeobrachaelurus* sp. 2; Landemaine, p. 11, fig. 3j–k.
1995 *Palaeobrachaelurus* sp.; Candoni, p. 39, figs 1–2.
1999 *Squatina alifera* Münster; Leidner and Thies, p. 32, fig. 1G; p. 36, fig. 3B–C.

Material. One tooth with damaged cusp, P. 65697; second similar tooth from Small Mouth Sands.

Description. The crown is wider than high and overhangs the root labially. A robust main cusp is flanked by wide and high lateral blades, each of which has a small cusplet about half way along their length, the entire occlusal edge (where seen) having a well-developed cutting edge. The basal edge of the lateral blades is rather concave. There is a very well-developed labial bulge, which is as wide as the main cusp and has a raised labial surface relative to the rest of the crown, which is flat. The lingual face of the crown is concave, other than where a poorly developed uvula is present as a thin enameloid covering on a slightly raised area of the lingual face of the root. The hemiaulacorhize root is at least as

wide as the crown, and is relatively high. The lingual face slopes lingually and has a very well-developed ventral foramen as well as a number of small lateral foramina. The basal face is relatively flat and distinctly V-shaped. The labial face of the root is strongly excavated and has very large medio-internal foramen. A large medio-external foramen is present at the lingual apex of the root.

Remarks. This tooth differs from a specimen removed from an articulated specimen of an adult *Squatina alifera* only in being slightly wider (Leidner and Thies 1999), a difference which would be expected within the low degree of heterodonty shown by extant *Squatina* species. The general tooth morphology is very atypical of extant *Squatina*, the low crown, lateral cusplets and high root all being more typical of orectolobiform teeth. This is even more marked in the teeth of juvenile *S. alifera* (=*S. speciosa* Meyer), which have well-developed lateral cusplets, no clear labial bulge and no lateral blades (see Leidner and Thies 1999), making them very similar to teeth of some orectolobiforms and heterodontiforms. The differences in tooth morphology between *S. alifera* and extant *Squatina* suggest that it may be appropriate to refer *S. alifera* to a different genus. Referral to another genus is, however, considered beyond the scope of this study until a re-examination of the skeletal remains of *S. alifera* has been carried out. There is a close similarity between the teeth of adult *S. alifera* and teeth of the presumed orectolobid *Palaeobrachaelurus* Thies, 1983. Although generally very similar to *Palaeobrachaelurus bedfordensis* Thies, 1983 (including *P. alisonae* Thies, 1983; Batchelor and Ward 1990), *S. alifera* teeth may be distinguished by the combination of small lateral cusplets and well-developed labial bulge.

Occurrence. Immediately below Wyke Siltstone.

Squatina ? *frequens* sp. nov.

Plate 4, figures 3–13

? 1983 *Squatina* sp.; Thies p. 108, pl. 11, figs 5–6.
1990 *Squatina* species A; Batchelor and Ward, p. 188, fig. 1.
1995 '*Squatina*' sp.; Candoni, p. 39.
1999 Squatinidae gen. et sp. nov.; Leidner and Thies, p. 32, figs 1H–I; p. 37, fig. 3D.

Derivation of name. From the high abundance of this species.

Holotype. P. 65698.

Material. Over 500 teeth, the majority poorly preserved, including P. 65699–65700, P. 65703–65704; also P. 65701 from Small Mouth Sands.

Diagnosis. Teeth roughly cruciform with single robust elongate cusp. The labial profile is symmetrical except in posterolateral files where the cusp is slightly angled to the posterior. The cusp is flanked by a pair of lateral blades which are shorter than the cusp in all but the most posterior teeth. Lateral blades are strongly separated from the upper surface of the root, and frequently have incipient cusplets at their

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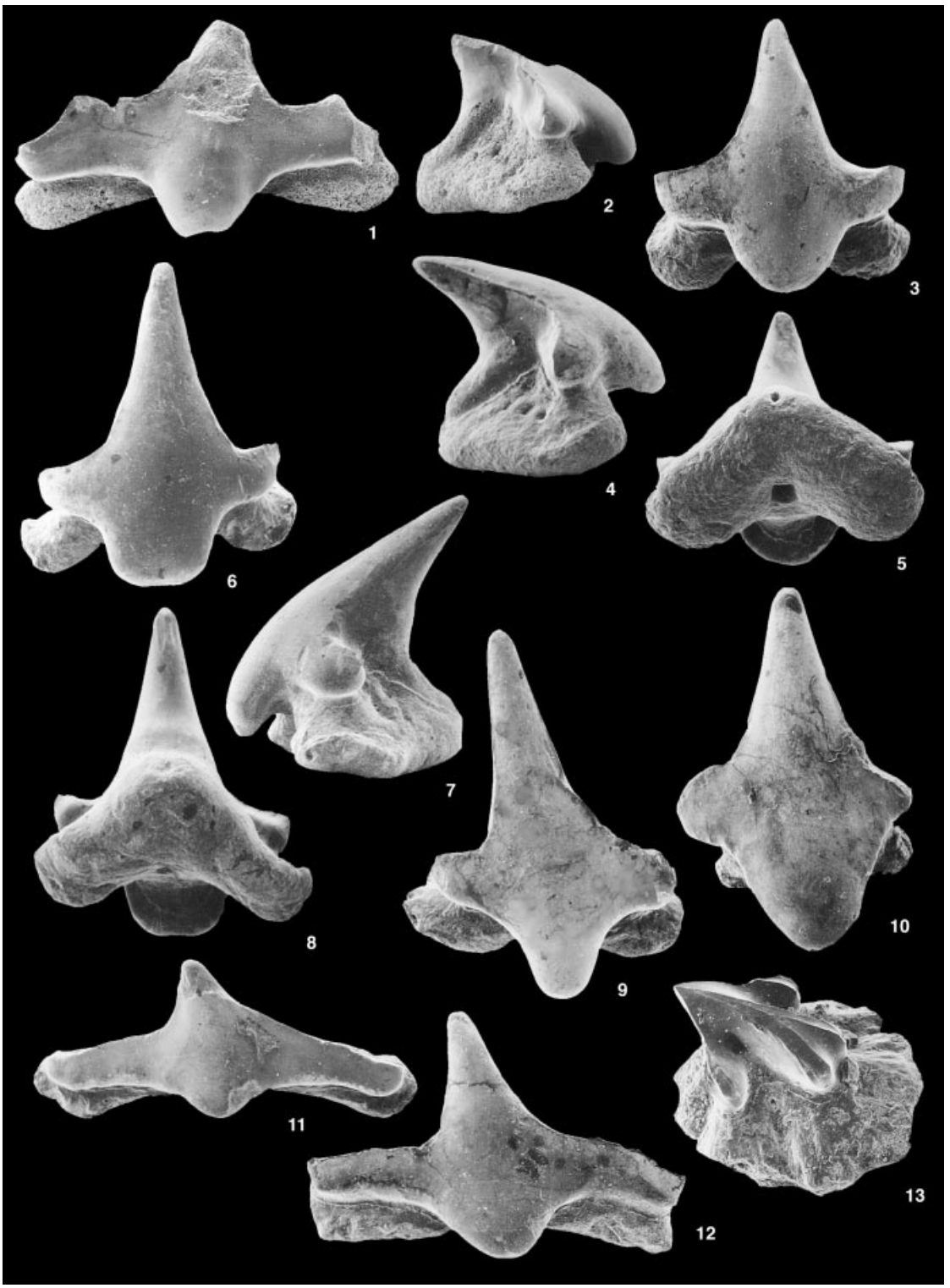
EXPLANATION OF PLATE 4

All specimens from lens between Wyke and Black Head siltstones unless stated otherwise.

Figs 1–2. *Squatina alifera* (Münster, 1842), P. 65697, immediately below Wyke Siltstone, lateral tooth, width 2·1 mm; ×27. 1, labial view. 2, lateral view.

Figs 3–13. *Squatina*? *frequens* sp. nov. 3–5, P. 65698, holotype, height 1·6 mm; ×28. 3, labial view. 4, lateral view. 5, lingual view. 6–8, P. 65699, height 2·1 mm; ×24. 6, labial view. 7, lateral view. 8, lingual view. 9, P. 65703, tooth of juvenile, labial view, height 1·3 mm; ×45. 10, P. 65700, possible symphyseal tooth, labial view, height 1·3 mm; ×45. 11, P. 65701, probable commisural tooth, Small Mouth Sands, labial view, width 2·4 mm; ×26. 12, P. 65703, lateral tooth, labial view, width 2·1 mm; ×29. 13, P. 65704, placoid scale, length 1 mm; ×45.



UNDERWOOD, *Squatina*

extremities. A labial bulge is very well developed, being as wide as the base of the cusp. There is no well-developed uvula, but enameloid covers the lingual face of the root below the cusp, not reaching the basal face of the root. The hemiaulacorhize root is high and at least as wide as the crown. The basal face is strongly V-shaped and slightly flared distally. Median foramina are very prominent, and at least two pairs of foramina are present on the lingual face of the root.

Description. The range of tooth morphologies recognised suggests that this species had rather weak monognathic heterodonty. The majority of the teeth recovered have a crown that is higher than wide and are bilaterally symmetrical, with a minority being wider with a somewhat angled cusp. The cusp is straight and triangular with a rounded cross section and a weak but continuous cutting edge. This continues onto the lateral blades, which are well developed and relatively parallel-sided. These often have a pair of incipient cusplets at the ends. A large labial bulge is present opposite the cusp. The labial bulge is somewhat variable in shape, generally being nearly semicircular and about the same width as the base of the cusp. The crown overhangs the root, especially along the labial edge and at the tips of the lateral blades. The root is high and somewhat displaced lingually, and is the same width or wider than the crown. An elongate apron of enameloid covers a somewhat raised ridge on the lingual face of the root. The basal face is convex in most teeth, becoming rather flatter toward the lateral extremities of larger and more posterior teeth, where it is frequently flared. A very large medio-internal foramen is present, with a smaller but well-developed medio-external foramen at the lingual apex of the root. The lingual face of the root has two pairs of foramina, more being present in posterior teeth. A single symphyseal? tooth has the lateral blades reduced to rounded projections separated from the narrow root and a very large triangular labial projection.

Remarks. The teeth of this species are here tentatively referred to *Squatina*, to which it has previously been referred (e.g. Batchelor and Ward 1990). In detail, these teeth differ significantly from those of *Squatina squatina* (Linnaeus, 1758) and other extant species in a number of respects. These include the possession of a high root with a strongly excavated labial side, lack of a flat base to the root in most teeth, incipient cusplets on the lateral blades, lateral blades strongly overhanging the root, lack of a well-developed uvula, narrow crown in most files and probable presence of specialised symphyseal teeth. Based on tooth morphology alone, this species closely resembles the Cretaceous orectolobiform *Cretorectolobus* Case, 1978. Despite this similarity, this species is provisionally referred to *Squatina* owing to the recognition of teeth conspecific with *S.*? *frequens* sp. nov. from skeletons referred to Squatinidae gen. et sp. nov by Leidner and Thies (1999). Both of the skeletons studied by Leidner and Thies (1999) are poorly preserved (Thies, pers. comm. 2000), and it is not impossible that further study may suggest an orectolobid affinity for these remains. Placoid scales extracted from the same skeletal remains are unlike those of other Jurassic *Squatina* specimens (Leidner and Thies 1999), and may further suggest the non-*Squatina* origin of the teeth. Similar placoid scales were collected in large numbers during this study, associated with the teeth of *S.*? *frequens*. Although rather distantly related, the extreme convergence in tooth morphology between *Squatina* and some orectolobiforms is well known within both extant and fossil taxa (e.g. Herman *et al*. 1992).

It is uncertain whether these teeth are conspecific with '*Squatina*' sp. of Thies (1983), the figured specimens of which could be accommodated within the morphological extremes of *S.*? *frequens*, but could not be considered typical. Teeth of *Squatina acanthoderma* Fraas 1854 have not been well figured, but appear to lack the incipient lateral cusplets of *S.*? *frequens* and be more inclined to the posterior. *S. acanthoderma* also has very different placoid scales, being of a morphotype not recorded during this study. Teeth of *Cretorectolobus doylei* Underwood *et al.*, 1999*a* are also similar to those of *S.*? *frequens*, but can be recognised in having a far smaller labial bulge and lateral blades more closely attached to the root.

Occurrence. Present in all samples, usually as the commonest selachian species. It is also very common at Small Mouth Sands.

Order RAJIFORMES Berg, 1940
Family RHINOBATIDAE Müller and Henle, 1838 *s.l.*

Remarks. It is probable that the Rhinobatidae Müller and Henle, 1838, *sensu* Cappetta 1987 constitutes a paraphyletic group (e.g. McEachran *et al.* 1996; Shirai 1996), with *Spathobatis, Belemnobatis* and

probably *Squatirhina* forming a clade of stem group batoids (Underwood *et al.* 1999*a*). This is separated from all extant rhinobatids by the possession of a primitive cranial skeleton and two dorsal fin spines (Brito and Séret 1996).

Genus SPATHOBATIS Thiolliere, 1854

Type species. *Spathobatis bugesiacus* Thiolliere, 1854 from the Upper Jurassic of France.

Spathobatis bugesiacus Thiolliere, 1854

Text-figure 5A–I

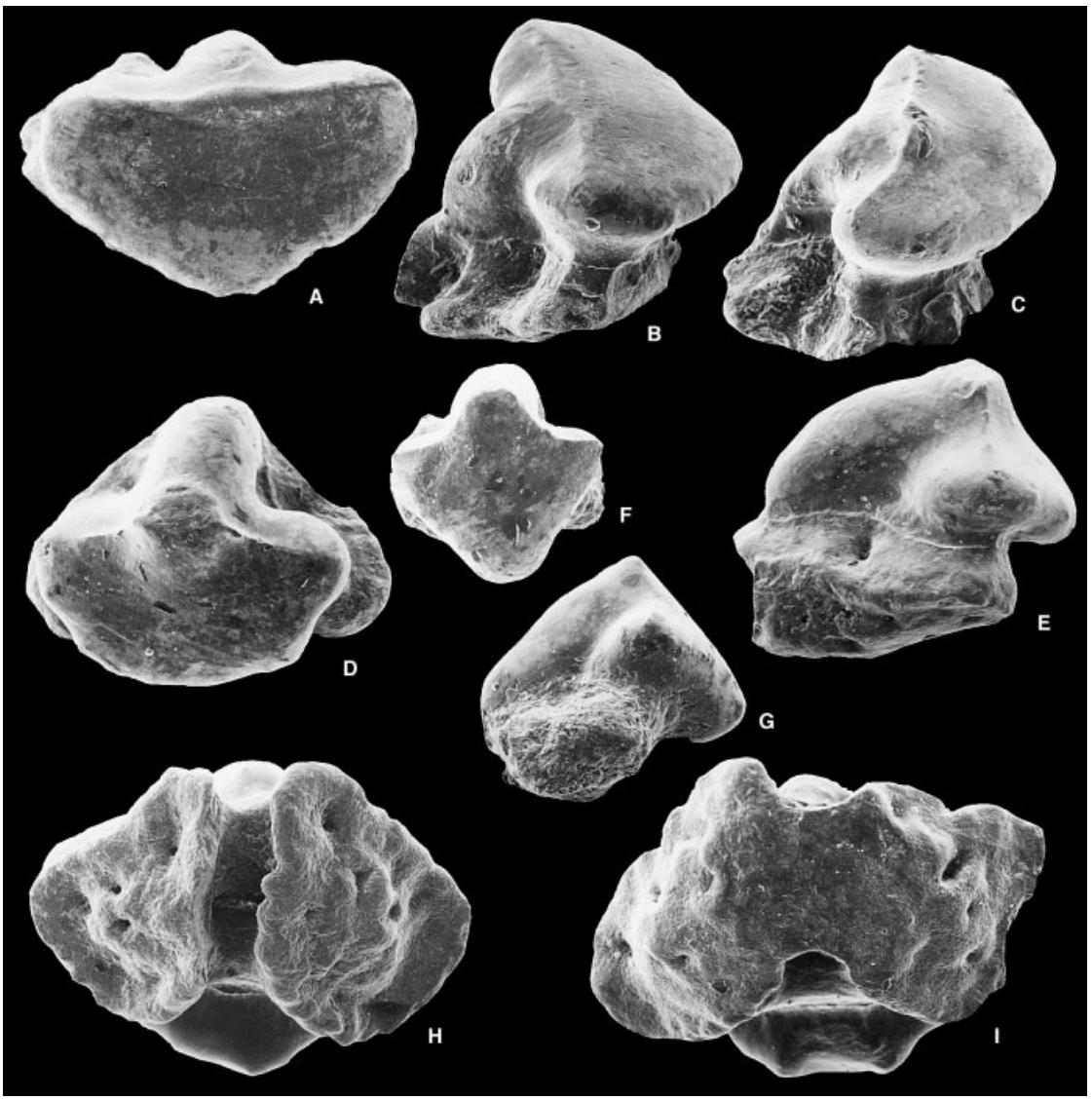
1854	*Spathobatis bugesiacus* Thiolliere, p. 7, figs 1–2.
1949	*Spathobatis bugesiacus* Thiolliere; Saint-Seine, p. 45, fig. 25.
1983	*Spathobatis bugesiacus* Thiolliere; Thies p. 45, text-fig. 6.
1983	*Spathobatis*? *uppensis* Thies, p. 111, fig. 5; p. 113, fig. 1.
1983	*Spathobatis*? *mutterlosei* Thies, p. 113, figs 2–4.
1983	*Spathobatis*? sp. 1; Thies, p. 113, fig. 5; p. 115, figs 1–3.
1983	*Spathobatis*? sp. 2; Thies, p. 115, figs 4–5.
1987	*Spathobatis bugesiacus* Thiolliere; Cappetta, p. 139, figs B–D.
1995	*Spathobatis uppensis* Thies; Candoni, p. 38.
1995	*Spathobatis mutterlosei* Thies; Candoni, p. 38.
1995	*Spathobatis werneri* Thies; Candoni, p. 38.
1995	*Spathobatis bugesiacus* Thiolliere; Cavin *et al*., p. 265, figs 2–6.
?1995	*Asterodermus* sp. 1; Thies, p. 472, figs L–O, p. 474, figs A–E (scales).
?1995	*Asterodermus* sp. 2; Thies, p. 474, figs F–G (scales).
?1995	*Asterodermus* spec. indet.; Thies, p. 476, figs A–D, G, J–K (scales).
1999	*Spathobatis bugesiacus* Thiolliere; Leidner and Thies, p. 35, fig. 1E (scales).

Material. 49 complete and partial teeth including P. 65705–65706, P. 65709–65710, also P. 65707 and P. 65708 from Small Mouth Sands.

Description. The population of teeth recovered during this study suggests that dentition of this species is far more heterodont than has previously been realised. Heterodonty appears to comprise both strong gradient monognathic variation and moderate sexual heterodonty, the latter indicated by the presence or absence of a small erect conical cusp, the presence of a cusp presumably indicative of teeth of males. The variations in crown morphology have been well documented by Thies (1983), in which teeth of differing position in the jaw were referred to different taxa. Extreme anterior teeth (*S*.? *uppensis* of Thies 1983) are relatively uncommon, and may represent a small number of files, as they are not recognised by Cavin *et al*. (1995). The crown is higher than wide, with an angle of 90 degrees or less between the lingual and labial faces. The uvula is especially well developed and at least as long as the tooth crown. The root is high and globular, with two well-defined root lobes. Anterolateral teeth (*S*.? *mutterlosei* of Thies 1983) have a crown that is at least as wide as high. The lingual edge of the crown is curved with little sign of a differentiated lingual apron, whilst the labial edge has a variable sized globular or conical cusp with straight or concave faces lateral to this. A well-developed edge separates the lingual and labial faces of the crown. The uvula is very well developed and at least as wide as the cusp. The root is lower than in anterior teeth and is at least as wide as the crown. The basal face is flat and may be angled laterally. Lateral teeth (*S*.? sp. 1 and *S*.? sp. 2 of Thies 1983) are wider than high. The crown is similar to that of anterolateral teeth, with a clear differentiation between teeth with or without a cusp. The uvula is smaller than in other teeth, but is still very well developed. The root is low and somewhat displaced labially. The flat-based root lobes are generally separated by a wide nutritive groove, although this is secondarily closed over in a fairly high proportion of teeth.

Placoid scales probably referrable to this species are not uncommon. These are variable in form, with most of the morphotypes recognised by Thies (1995) as *Asterodermus* spp. being present. The material collected here adds nothing to the descriptions of Thies (1995). It seems highly likely that the association of these batoid scales with teeth of *Spathobatis bugesiacus* at two localities in Germany and in Dorset suggests that they are synonymous.

Remarks. Many of the teeth described here, as in Thies (1983), are inseparable from those extracted from entire skeletons of *Spathobatis bugesiacus* known (Cavin *et al.* 1995, figs 2–6). The degree of heterodonty



TEXT-FIG. 5. All specimens from lens between Wyke and Black Head siltstones unless stated otherwise. A–I, *Spathobatis bugesiacus* Thiolliere, 1854. A–B, P. 65709, lateral tooth of female, width 0.8 mm; × 70. 1, occlusal view. 2, oblique lateral view. C, P. 65710, lateral tooth of male, oblique lateral view, width 0·6 mm; ×85. D–E, P. 65705, anterior tooth of male, width 0·8 mm; ×55. D, occlusal view. E, lateral view. F–G, P. 65706, extreme anterior tooth, width 0·5 mm; ×55. F, occlusal view. G, lateral view. H, P. 65707, tooth with open nutritive groove, Small Mouth Sands, width 0·9 mm; ×62·5. I, P. 65708, tooth with closed nutritive groove, Small Mouth Sands, width 1 mm; ×62·5.

exhibited by *S. bugesiacus* has not previously been recognised, having been partly concealed by the taxonomic splitting of the tooth assemblages collected by Thies (1983). There are several reasons why these species are here considered synonymous. Morphological intermediates between the various 'species' are present within the material described here, as in the Kimmeridgian of northern France, where it was recognised as impractical to separate all but the morphological extremes (Candoni 1995). It would be highly unlikely that several related species would be present in similar proportions across Europe, but the

same morphotypes are present in similar proportions in three German localities (Thies 1983), northern France (in which the lateral teeth are referred to *S. werneri* Thies; Candoni 1995), and Dorset. Other highly heterodont 'rhinobatids' have recently been recognised in the British Lower Cretaceous (Underwood *et al.* 1999*b*; Underwood and Rees in press). Lateral teeth are very similar to teeth of *Belemnobatis sismondae* Thiolliere, which co-occurs with *S. bugesiacus* in France. Teeth of *B. sismondae* may be separated by the presence of a more gracile uvula, slightly flared lateral edges of the crown and lower root (Cavin *et al.* 1995). The status of *Asterodermus platypterus* Agassiz, 1843 is currently uncertain, but it is likely to be conspecific with *S. bugesiacus*. The holotype lacks a head, and cannot be recognised on placoid scale morphology (Leidner and Thies 1999), but the skeletal structure has not been studied in detail.

A variety of placoid scales has been described as species of *Asterodermus* by Thies (1995). These were associated with the teeth he described as species of *Spathobatis* (Thies 1983) and are very likely to be synonymous with them and hence with *S. bugesiacus*. A very similar range of scale morphotypes was recorded during this study, as well as from articulated skeletons assigned to *S. bugesiacus* and *A. platypterus* (Leidner and Thies 1999).

Occurrence. Present in all samples from the Wyke and Black Head siltstones; also frequent at Small Mouth Sands.

Superorder HOLOCEPHALI Bonaparte, 1832
Order CHIMAERIFORMES Patterson, 1965
Family CHIMAERIDAE Woodward, 1891

Genus ISCHYODUS Egerton, 1843

Type species. *Chimaera townsendii* Agassiz, *in* Buckland, 1835 from the Tithonian of England.

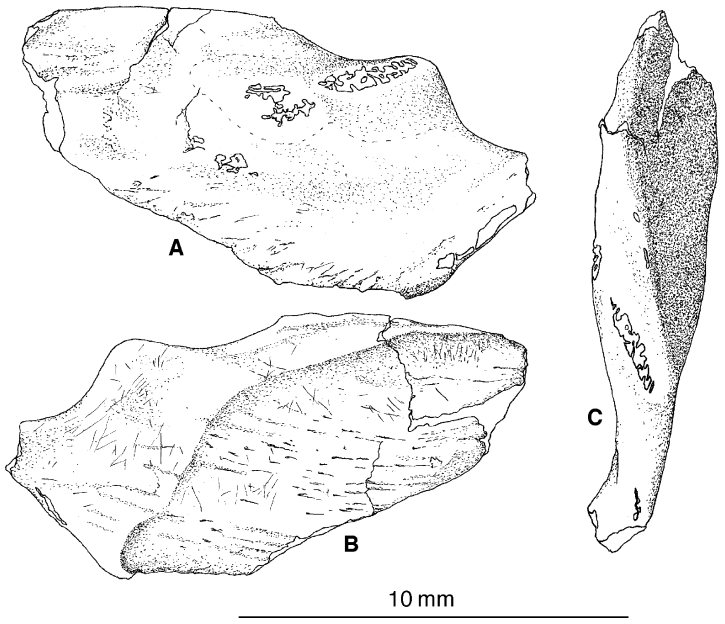
Ischyodus sp.

Text-figure 6A–C

Material. One mandibular plate P. 65713.

Description. This small plate, only 13 mm in length, is relatively well preserved, lacking only the mesial extremity and with some damage along the lingual and symphyseal margins. Faint striations on the basal face of the plate appear to be taphonomic, caused by the teeth or radula of a scavenging animal. The plate is rather rhombohedral in profile and strongly occluso-basally flattened. The anterior labial margin is sinuous with a strongly projecting labial edge of the anterior outer tritor. The posterior labial margin is long and slightly convex. The symphyseal margin is short and strongly divergent from the posterior labial margin. The posterior labial margin is somewhat curved occlusally, but lacks a well-developed outer tritor. The labial margin is long and irregularly convex. The anterior outer tritor is moderately well developed and elongate but low. This is only slightly separated from the median tritor, which is low and relatively poorly developed. A weakly raised area is present on the lingual side of these tritors. The symphyseal margin is curved occlusally and no clearly defined tritors are visible, although it is possible that some of the damage in this region is because of wear of poorly defined tritoral areas. The basal face shows a well-developed descending lamina, extending from the posterior edges of the symphyseal and labial margins. The labial edge of this is well defined for much of its length, being least prominent to the posterior of the mesial apex. A faint ridge and groove are present along the posterior labial margin. The posterior part of the basal surface is clearly vascular, and is somewhat curved basally towards its lingual extremity.

Remarks. The poorly developed tritors and low degree of wear on this specimen suggests that it represents the tooth plate of a juvenile individual. Numerous nominal species of chimaeroids have been described from the European Upper Jurassic, including a number of taxa referred to *Ischyodus* (at least 12 species according to Woodward 1891). In many cases, the descriptions and figures of these taxa have been poor, and it is probable that little allowance has been made for ontogenetic and other intraspecific variation, which is known to be considerable in some extant chimaeroids (Dean 1906; Didier and Nakaya 1999). The



TEXT-FIG. 6. A–C, *Ischyodus* sp., P. 65713, lens between Wyke and Black Head siltstones, mandibular plate. A, occlusal view. B, basal view. C, labial view.

common practice of using the form of the tritors as diagnostic features ignores the biological factors which effect tritoral shape, and hence may lead to spurious taxonomy (Stahl 1999). It is therefore probably inadvisable to refer small and probably juvenile tooth plates to these nominal taxa without a re-appraisal of the type and referred material.

Occurrence. Lens between Wyke and Black Head siltstones.

PALAEOECOLOGY

Although superficially rather homogeneous, the Lower Kimmeridge Clay of Dorset contains a range of discrete faunal assemblages indicating a diversity of palaeoenvironments (e.g. Wignall 1990*b*). The shelly clays of the lower Kimmeridge Clay are completely bioturbated and contain a very rich and diverse invertebrate fauna. The sandy clays at the base of the unit contain abundant large epifaunal suspension feeders (especially the oysters *Deltoideum* and *Nanogyra*, serpulids and the brachiopod *Torquirhynchia*), as well as common infaunal bivalves (especially *Thracia* and *Pleuromya*), mobile epifaunal taxa (cidarid echinoids and diverse gastropods) and ammonites. Less sandy clays, such as the shelly lens below the Wyke Siltstone, typically contain a less diverse epifauna (although still dominated by oysters) and more diverse infaunal bivalve assemblage. The shelly sandstone lens between the Wyke and Black Head siltstones also contains a rich and diverse invertebrate fauna. This represents a death assemblage with no fossils seen to be in life position. Within this lens *Deltoideum* is very rare, but *Nanogyra* and serpulids are common. Small gastropods, infaunal bivalves and fragments of small echinoids are common and diverse. The base of the lens is heavily bioturbated with common *Planolites*, *Rhizocorallium* and ?*Diplocraterion.* As well as this typical Kimmeridge Clay assemblage, rare fragments of colonial corals were observed, although the occurrence of these as abraded fragments suggests that they are probably transported or reworked. It is therefore evident that the Kimmeridgian elasmobranchs formed part of rich and diverse palaeocommunities, with a diversity of potential food sources.

The diversity of elasmobranch and other fish remains within the Kimmeridgian of Dorset suggests that fish with a wide variety of feeding strategies filled a complex suite of niches. It is not, however, readily possible to quantify the biomass of fish at different trophic positions. This is due to both taphonomic effects and the differing rates of tooth production of different taxa. There is likely to be considerable time-averaging within the rock units where vertebrate remains are concentrated, and it also has to be noted that the differential preservation of teeth within the assemblages may suggest that some material has been transported from other, nearby, environments. Differential production rates of teeth are likely to have allowed chimaeroids to be strongly underrepresented in the preserved fauna. An individual chimaeroid would have produced only six tooth plates and one fin spine during its lifespan, as opposed to the production and shedding of several hundreds or thousands of teeth during the lifespan of sharks and rays. Despite these reservations, it is possible to analyse the composition of the fauna in very general terms.

It is evident that there were numerous taxa capable of consuming hard-shelled food items (heterodontiforms, *Protospinax*, *Spathobatis*, and probably *Ischyodus* as well as semionotid and pycnodont actinopterygians). Of these, the common incidence of high levels of tooth wear in heterodontiforms and *Spathobatis*, suggest that these groups were commonly durophagous. These probably fed on benthic molluscs, echinoderms and crustaceans, as well as possibly on ammonites, all of which are common as fossils associated with the elasmobranch material. These forms were probably all largely benthic. ?*Squatina* was probably also benthic like extant *Squatina* and *Orectolobus*, its clutching-type dentition (of Cappetta 1986) suggesting that it most likely represented an ambush predator. It is probable that *Synechodus* fed in a similar way, but had a dentition also capable of breaking down some shelled prey items. Ambush predators were therefore probably well represented within the fauna.

It is likely that *Palaeoscyllium* fed largely on small prey items, but may also have been something of a generalist. Similar diets could be expected for some of the rare orectolobiformes and possibly for juvenile *Paracestracion*, as well as many of the actinopterygian taxa. The larger hybodonts, with their clutching or tearing dentitions, were active predators of fish and cephalopods. By comparison with other hybodonts, however, it is unlikely that the species recorded here were either very large (under 1·5 m long) or fast swimming. Along with actinopterygian taxa such as members of the Pachycormidae, it is likely that these hybodonts caught their prey through rapid acceleration rather than straight pursuit. Despite the presence of these moderate-sized predators, it is certain that the top carnivores would have been marine reptiles such as pliosaurs, ichthyosaurs and crocodilians, the remains of which are common and diverse within the Kimmeridge Clay.

COMPARISON WITH OTHER FAUNAS

The elasmobranch faunas of the Kimmeridgian of Dorset appear to be amongst the most diverse known from the Jurassic. Despite this, they are in many ways similar to associations from other open marine deposits from the Middle and Upper Jurassic and much of the Lower Cretaceous. These typically comprise moderate diversity assemblages of small heterodontiforms, orectolobiforms, *Protospinax*, *Synechodus* and 'rhinobatids'; *Sphenodus*, *Squatina*, hexanchids, scyliorhinids and larger hybodonts are also frequently present, as are small to medium-sized chimaeroids. These faunas have been recorded from neritic mudstones in the Toarcian of Belgium (Delsate and Lepage 1990), Aalenian of Germany (Thies 1983), Callovian of England (Thies 1983; Martill 1991), Kimmeridgian of France (Candoni 1995) and Hauterivian of England (Underwood *et al.* 1999). Faunas observed from inner shelf carbonate settings, such as the Bathonian of England (Young 1982 and pers. obs.) and Tithonian of France (Candoni 1995) share many similarities, but these tend to differ in containing far fewer orectolobiforms and lack palaeospinacids, but have a higher diversity and abundance of small hybodonts. Palaeospinacids and orectolobiforms are likewise rare within plattenkalks, which may represent environments that were both shallow and somewhat restricted. Tithonian plattenkalks in Germany contain a diverse elasmobranch fauna (e.g. Schweizer 1964) within which batoids, heterodontiforms and *Squatina* are especially well represented, whereas Kimmeridgian plattenkalks from France (Saint-Seine 1949) contain abundant batoids almost to the exclusion of other elasmobranchs. Deposits representing conditions of reduced salinity contain diverse hybodonts and common batoids, as in the Kimmeridgian of Germany (Duffin and

Thies 1997) and Berriasian of England (Underwood and Rees in press), with batoids being absent in near freshwater conditions.

Although there has been little work conducted on the palaeoecology of early neoselachians, the close relationship between elasmobranch faunas and facies suggests that Jurassic and Lower Cretaceous taxa were strongly environmentally controlled. Palaeospinacids, scyliorhinids and hexanchids appear to have been largely restricted to deeper water environments where the sea-floor was below storm wave base, whilst orectolobiforms appear to have been at their most abundant and diverse within these settings. Heterodontiforms and *Squatina* appear to have been most abundant within shallower carbonate shelves, the high frequency of both within German plattenkalks possibly suggesting a close affinity with the reef habitats that fringed the lagoon complex in which these rocks were deposited. The almost ubiquitous occurrence of *Protospinax* within Jurassic marine sediments possibly suggests that it was a very cosmopolitan taxon. 'Rhinobatids' also appear to have been cosmopolitan, with a greater tolerence of restricted conditions than other neoselachians. Although large hybodonts appear to be present within most marine environments, the increase in number and diversity of smaller hybodonts (especially *Lissodus s.l.*) in nearshore and reduced salinity settings suggests that they dominated these marginal marine environments.

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